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THE FAUNA OF QUARRY NINE.

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INTRODUCTION.

The famous "Quarry 9" in the Morrison Formation at Como Bluff, in southern Wyoming, was opened in 1879 by Mr. William Reed, field assistant to Professor Marsh, and was worked by him and his assistants and successors more or less continuously for about six years. During this time it yielded not only the most important fauna of Mesozoic mammals ever discovered, but also a remarkable suite of small forms of other classes. The singular variety of this fauna is evident from the fact that every order of non-marine vertebrates known to have been in existence during upper Jurassic time is represented in the collections from this one quarry! Of the Morrison mammals, all but five were derived from this one lens of clay.

Many of these mammals and other vertebrates were described by Prof. Marsh (see bibliography at end of paper), while various of them have since been the subjects of papers by Gidley, Moodie, Gilmore and the present writer. In 1909 Gilmore published a preliminary résumé of the fauna and stated that in a later communication he hoped to present a more detailed account, a promise which he has not since had an opportunity to fulfill. Although it is not yet possible to give a thorough revision of all the available material, a brief study emending and adding to Gilmore's faunal list and considering it ecologically seems worth while.

FAUNAL LIST

In the following list an asterisk preceding a name indicates that the holotype of the species so marked was derived from this quarry.

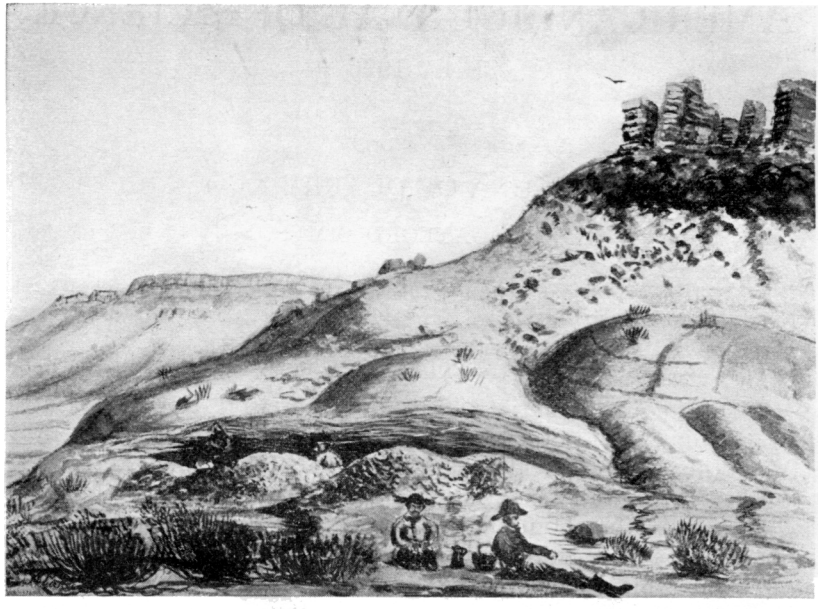

Fig. 1. Marsh's Field Party at Quarry 9. From a hitherto unpublished contemporary colored drawing by Arthur Lakes.

INVERTEBRATA

MOLLUSCA

Gastropoda

Cf. *Planorbis* sp.

Pelecypoda

Unio sp.

VERTEBRATA

PISCES

**Ceratodus güntheri* Marsh

Numerous fish jaws and vertebrae, mostly unidentified ganoids.

AMPHIBIA

**Eobatrachus agilis* Marsh

REPTILIA

Chelonia
Glyptops ornatus Marsh
Rhynchocephalia
**Opisthias rarus* Gilmore
**Theretairus antiquus* Simpson
Crocodilia
Goniopholis sp.
Saurischia
Morosaurus sp.
Coelurus fragilis Marsh
Antrodemus sp.
Several other carnivorous dinosaurs, not precisely identifiable.
Ornithischia
Laosaurus gracilis Marsh
Laosaurus ?consors Marsh
Dryosaurus altus Marsh
Stegosaurus sp.
**Macellognathus vagans* Marsh
Pterosauria
**Dermodactylus montanus* Marsh
Lacertilia
Some of the many small reptilian jaws probably belong here.[1]

AVES

**Laopteryx priscus* Marsh

MAMMALIA

About twenty-two genera, representing all the known Jurassic orders. They are being revised elsewhere by the writer.

NOTES ON THE FAUNAL LIST.

Although so abundant, the bones from this quarry are always dissociated, a fact which makes their determination difficult. The shells are represented only by very imperfect rusty impressions and casts, but these are fairly numerous, especially the *Unio's* which are small, averaging about 3 cm. in length.

[1] They will be referred to by Gilmore in a forthcoming work on fossil lizards.

The recent study of Moodie has established *Eobatrachus* as an undoubted anuran of modern type. It may (according to the reader's belief as to the age of the Morrison) share with *Montsechobatrachus gaudryi* (Vidal) the honor of being the oldest known frog, the latter being of Kimmeridgian age. The chelonian material is very abundant and of varying size, including some essentially complete carapaces. The crocodilian material is not less abundant, but rather less perfect. The larger dinosaurs, as *Morosaurus* and *Stegosaurus*, are represented only by one or two teeth. There are very numerous teeth of carnivorous dinosaurs of all sizes and it is probable that most or all of the characteristic Morrison genera are represented, but it is not possible to identify them by such isolated material. A few limb bones also occur. The smaller ornithopods are represented by a number of limb bones, but the largest forms of this group appear to be absent.

Although it has not received wide recognition, *Dermodactylus*, the first American pterosaur, is represented by scanty but very characteristic material. The status of *Laopteryx* is less certain and further study is necessary before it will be possible to affirm or deny its avian nature in a definitive manner.

STRATIGRAPHY.

A detailed section of the Como Bluff Morrison has been given by Loomis (1901) and he states that the mammal layer (which is that which has yielded all the forms listed above) is a six-inch band of clay occurring just beneath a four-foot bed of sandstone, the latter being No. 24b of his section. This indicates the horizon as near the middle of the Morrison at this place, about eighty feet below the Dakota (Cloverly?) and about eighty-five feet, or possibly more, above the marine Jurassic. The Morrison being a continental deposit of very variable character, this information is at present of no use in correlation. It is only by the accumulation of numerous faunal lists of known position and narrow vertical range that a sequence of faunas will be made out in the Morrison, if such exists.

PALEOËCOLOGY.

As is often, indeed usually, the case, a simple perusal of the faunal list of Quarry 9 does not give an adequate idea of the actual animal association. Thus, although several large

forms, even including *Morosaurus,* appear, they certainly do not belong to this ecological group, while remains of some of the smaller ones are very rare. It is also certain that a number of types of organisms not mentioned in the faunal list were present and they must be included in a study of the fauna even though they are not preserved as fossils.

There are two more or less distinct subfaunal units or cenobiotas,[2] affecting each other very frequently, it is true, but on the whole independent. The first comprise the aquatic and thoroughly amphibious animals, the *Unio's,* the fish, the frogs, the turtles, and the crocodiles. The other group, the small fauna of the land of the Morrison region, consists of the rhynchocephalians, the small dinosaurs, the pterodactyls, the lacertilians, the birds, and the mammals. All the animals mentioned were probably common enough to be of importance at the time, as those which are very rare in our collections (frog, pterodactyl, bird) are just those of which the smallest percentage of individuals are fossilized in all formations.

The first step in the energy cycle which this fauna presents is obviously now missing as it must have consisted of green plants, as in all cases. There are numerous brown to black carbonized or sometimes rusty films and irregular impressions in the clay matrix which must betoken a considerable development of aquatic, and no doubt also terrestrial, vegetation. In the aquatic subfauna there are no exclusive herbivores, so that it is plain that here at least one other step is missing. The molluscs, chiefly *Unio's,* fed on microscopic organisms, both plant and animal. The lung fishes fed on small molluscs, on crustaceans, worms, etc.[3] The other fishes apparently did not eat molluscs or the harder and larger crustacea, but must have thrived on small crustaceans, aquatic worms and larvae, and also on such insects as became accessible to them. This complex of small invertebrates has left no fossilized trace, but its abundant presence and general character is as manifest as if all the details were known. The frogs also belonged to the

[2] Möbius (1893) suggested the word "biocönose" for use in this sense of a "lebensgemeinschaft." In adopting the word for use in English the form "cenobiota" (κοινός, common, βίος, life) seems preferable as very much more in harmony with the rest of the English scientific vocabulary. A cenobiota is a special sort of biota, or, from another point of view, one of the smaller units of which the general biota of a region is composed. Cenobiosis is an interspecific relationship much less intimate than symbiosis.

[3] It has been stated that the living *Neoceratodus* eats vegetable as well as animal food, but this appears to be incorrect, the plants being ingested solely for the sake of the small animal life clinging to them.

group of animals which subsisted chiefly on this small invertebrate diet. It is probable that the frogs, especially when young, also served in another role less pleasant to them, namely that of a supplementary article of diet for the fishes and small turtles.

Our attention is thus turned to the next ecological element of the aquatic cenobiota, that of the highest carnivorous or vertebrate-eating animals, the ones farthest removed from the beginning of the energy cycle. The fish belong here only to a slight extent, although they undoubtedly ate tadpoles, frogs and smaller fish on occasion. The aquatic carnivores *par excellence*, however, were the crocodiles and turtles. As their limb structure clearly shows, the members of both of these groups were still well able to progress on land, but their chief source of food and their most congenial home was in the water and hence they are properly considered with the aquatic cenobiota.

The rather small crocodiles were surely exclusively carnivorous, eating on the one hand fish, frogs, and other adequately large aquatic animals, and on the other such mammals and small dinosaurs as were so unlucky as to fall into the water or so unguarded as to let themselves be carried thither. The possibility of a connection between the development of the crocodiles and of their prey was first pointed out by Owen (1879). The earlier true crocodiles were almost exclusively of longirostrine type, and not until the upper Jurassic did brevirostrine crocodiles become common. It is a notable fact, also, that in the upper Jurassic the latter were markedly smaller than their contemporaneous long-snouted cousins and also smaller than their Tertiary and recent short-snouted relatives. That the spread of brevirostrines at this particular time and their small size were associated with a simultaneous expansion of small animals suited to be their prey is a natural assumption. If we compare the food habits of modern forms, it is found that the longirostrines are largely or exclusive piscivorous while the brevirostrines are also in part fish-eating but often depend largely upon higher prey, especially mammals. The conclusion is very tempting that the spread of Mesozoic mammals in the late Jurassic was a factor in the simultaneous spread of small brevirostrine crocodiles. Whether the causal connection was actually so close or not, and one prefers not to commit oneself on such scant evidence, it seems certain that the crocodiles of the upper Jurassic were admirably suited to prey on the small contemporaneous mammals and they quite surely did so. Owen has pointed out that the dwarf crocodiles *Nan-*

nosuchus and *Theriosuchus* are found in actual association with abundant mammalian remains in the Purbeck. The same is true of *Goniopholis* in both the Purbeck and Morrison. *Goniopholis* was rather larger, it is true, and an exceptionally favored individual might reach a length of some nine feet, but the average was considerably less. In the Quarry 9 material most of the crocodiles are of small size, ranging from infants of a foot or so up to adults of five or six feet in length. The largest would have no reason to scorn a mammal or a small land reptile as an article of diet. The skull proportions and dental characters are not significantly different from those of the most inveterate mammal-eaters among recent crocodiles.[4]

As is well known, the turtles of the present day (in a general sense, including also tortoises and terrapins) have the most various food habits. Those which inhabit fresh water, however, and which otherwise seem most nearly comparable to the Morrison forms (*Probaëna* and *Glyptops*) are almost exclusively carnivorous. Despite their inferior size, the food of the Quarry 9 turtles was probably comparable with that of the crocodiles to a large extent, although perhaps including smaller animals and even some vegetation. The ferocity and predaceous ability of the modern snapping turtle is well known.

In the aquatic cenobiota the crocodiles and turtles represent the highest point in the energy cycle. It is very unlikely that they were the prey of any other predaceous carnivores. Not only were they the largest forms of their cenobiota, but both were enclosed in a heavy bony armor, *Goniopholis* not being inferior to any turtle in this respect. After the death of one of these forms the energy stored in his tissues at that particular time would usually be returned at least in part to one of the earlier stages of the cycle.

Turning to the land, we find that the fundamental forms, the land plants, are again unknown from this quarry and very poorly known from any part of the Morrison Formation, but their abundance may safely be assumed. On them fed not only certain of the vertebrates, the laosaurs and the herbivorous mammals (multituberculates), but also, with the intervention of intermediate steps in many cases, all of the land invertebrates. On these latter in turn depended the pantotheres among the mammals and the rhynchocephalians and lacertilians among the reptiles, all of which were apparently of the dietetic type commonly, but rather inaccurately, styled

[4] Although, of course, they do not yet reach the extreme of this type as seen in the alligator.

insectivorous. While some may have been strictly insectivorous, the majority must have added to the latter other land arthropods, worms, etc. That no such invertebrate animals are known as fossils from the Morrison is a gap in our knowledge, but does not involve the slightest doubt as to their abundant presence at the time. As will be noted below, insects are

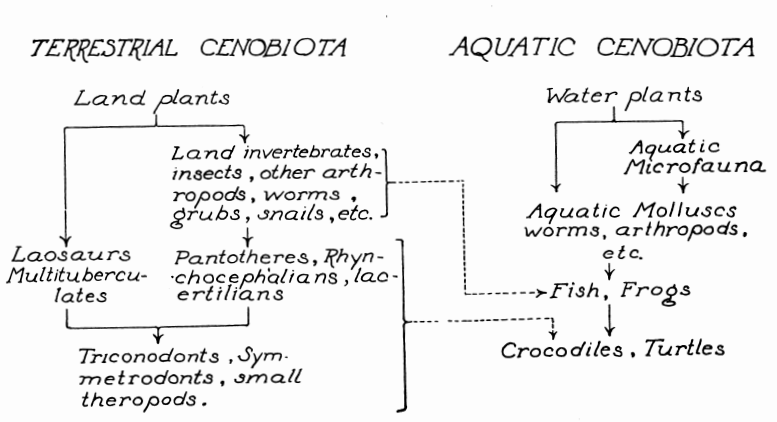

Fig. 2. Schema of the Paleoëcological Relationships of the Fauna of Quarry 9.

a rather common element in the English Purbeckian, a fauna essentially contemporaneous with that of Quarry 9 and of somewhat similar facies.

The smaller theropod dinosaurs and the symmetrodont and triconodont mammals were the predaceous carnivores of the terrestrial cenobiota, and they found their prey in the laosaurs, multituberculates, pantotheres, rhynchocephalians, and lacertilians.

There must have been numerous interactions between the terrestrial cenobiota and the aquatic one. Probably the most constant and important of these were in the first place the eating by the fish and frogs of the terrestrial invertebrates, and in the second place (and probably more significantly) the preying of the more properly aquatic carnivores upon the small land vertebrates of all groups, especially the mammals. All the relationships may be summed up in the diagram, Fig. 2, it being understood, of course, that such a schematic representation involves the omission of many intermediate steps and of

many details and variants in order to bring out the more fundamental features.

The arrows indicate the more accentuated lines of food derivation and energy flow.

PURBECK FAUNA AS A CONTROL.

The Purbeck beds of England contain an interesting fauna analogous in many respects with that of Quarry 9 and markedly confirming the ecological inferences drawn for the latter. In the case of the Purbeck, unfortunately, it is not possible to gather an adequate faunal list from a single bed, as has been done above for the Morrison, nevertheless the fauna of the freshwater strata of the middle Purbeck of the vicinity of Swanage, Dorsetshire, certainly comprises forms which it is safe to assume as sharing the same general environment. The facies is somewhat different due, among other factors, to the very close proximity of the sea and to the fact that the Purbeck waters were less dynamic and were limy rather than muddy, nevertheless the ecology is quite similar to that of Quarry 9. A very brief faunal synopsis follows:

INVERTEBRATA:

MOLLUSCA: Numerous brackish and fresh water gastropods and pelecypods.

INSECTA: Very numerous in the middle Purbeck, although most of them not specifically from Swanage. Coleoptera, Neuroptera, Diptera, Hemiptera, Orthoptera all well represented and two hymenopterans also found.

CRUSTACEA: Numerous ostracods, other crustaceans less well known but certainly present.

VERTEBRATA:

PISCES: Fish, almost exclusively ganoids, common, mostly of moderate size and representing a considerable variety of food adaptations. *Ceratodus* is not found, these waters being too close to the sea and not subject to such seasonal variation as were those of the Morrison.

REPTILIA: Chelonians very numerous, at least five genera being noted for the middle Purbeck of Swanage. Crocodiles also numerous, *Goniopholis* (three species or more) appearing to be the dominant form, but *Theriosuchus*, *Nannosuchus*, and *Oweniasuchus* being also common. The dinosaurs poorly represented, even the smaller ones being rare, due, no doubt, to the difference of facies from Quarry 9 as noted

above. *Nuthetes* and *Echinodon*, which appear to be respectively a small carnivorous dinosaur and a small herbivorous one, are, however, known from a number of specimens. Pterosaurs are rare but a distinct species of *Ornithochirus* is known. At least two small genera, *Macellodus* and *Saurillus*, are referred to the Lacertilia with sufficient sureness for ecological purposes. *Homoeosaurus*, the small rhynchocephalian, is reported from the Purbeck, but the exact locality and horizon is unknown to the writer.

MAMMALIA: The relatively large mammalian fauna of the Purbeck is very close to that of the Morrison, both in facies and in blood relationship, and presents on the whole the same adaptive types in about the same proportions.

It is thus seen that this fauna, also, shows in an interesting way an association of the type discussed above. Indeed, there are present as actual fossils some groups whose presence in the Morrison could only be inferred. The Purbeck thus forms an admirable check or control. It would in itself form an admirable subject for detailed study, as it is complicated to a considerable extent by the presence not only of a terrestrial cenobiota (less prominently developed than that of Quarry 9) and of a freshwater one (very similar to that of Quarry 9), but also of a marine one which occasionally invaded the region and between which and the freshwater cenobiota a series of extremely interesting gradational brackish phases occur. The marine and brackish groups have been omitted from the above brief notice, however, in order to facilitate clearer comparison.

RÉSUMÉ.

Quarry 9 of Professor O. C. Marsh's field parties at Como Bluff, Wyoming, has yielded a fauna remarkable for its variety and for being derived from a single thin lens of clay. This circumstance gives an exceptional opportunity to study the ecology of an extinct fauna very unlike any of to-day and constituting a unit in time and space more surely than is usually the case in dealing with fossils. It also gives a unique glimpse into the lives of the smaller and less well-known creatures of the middle of the Age of Reptiles.

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